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LETTER

How have recent temperature changes affected the efficiency of ocean biological carbon export?

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Scientific Significance Statement

The ocean's biologically mediated carbon reservoirs are an integral component of the global carbon cycle, and may feed back on climate if the total carbon exported out of the surface ocean is affected by surface temperatures. However, the magnitude of this feedback is difficult to quantify. Using long-term temperature records and a simple metabolic model, we show a 1.5% ± 0.4% decline in the fraction of primary production removed from the surface ocean over the past three decades of climate change, suggesting increased global temperatures have reduced the efficiency with which the ocean exports carbon into the deep. The larger temperature changes in Earth's history may have reduced this efficiency much more so.

Abstract

The ocean's large, microbially mediated reservoirs of carbon are intimately connected with atmospheric CO_2 and climate, yet quantifying the feedbacks between them remains an unresolved challenge. Through an idealized mechanistic model, we consider the impact of documented climate change during the past few decades on the efficiency of biological carbon export out of the surface ocean. This model is grounded in universal metabolic phenomena, describing export efficiency's temperature dependence in terms of the differential temperature sensitivity of phototrophic and heterotrophic metabolism. Temperature changes are suggested to have caused a statistically significant decrease in export efficiency of 1.5% ± 0.4% over the past 33 yr. Larger changes are suggested in the midlatitudes and Arctic. This interpretation is robust across multiple sea surface temperature and net primary production data products. The same metabolic mechanism may have resulted in much larger changes e.g., in response to the large temperature shifts between glacial and interglacial time periods.

The ocean's "biological pumps" sustain large reservoirs of carbon, mediated by microbial activity, with significant leverage on atmospheric CO_2 and climate (Volk and Hoffert 1985). While the general significance of the biological pumps for the carbon cycle and climate is clearly demonstrated (Volk and Hoffert 1985; Cox et al. 2000) the details

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Data Availability Statement: All data used in this manuscript are from publicly available sources. The metadata and specific data used in the analyses described in the text can be found at https://figshare.com/s/a7c01cb2a9853eca9b8c. All code used for analysis in this manuscript is available at http://cael.space.

Additional Supporting Information may be found in the online version of this article.

of their relationship remain elusive (Boyd 2015). Understanding the current functioning of the biological pumps is limited because in situ data is sparse (Boyd and Trull 2007), data collection is difficult and expensive, and the system is extremely complex and variable (Buesseler and Boyd 2009).

Even so, there exists a clear and quantifiable imprint of metabolic sensitivity to temperature in the ocean system (e.g., Eppley 1972), which can be exploited to understand global changes in carbon export with climate change. In particular, differential sensitivities of phototrophic and heterotrophic metabolisms to environmental temperature are documented (Eppley 1972; Huntley and Lopez 1992), and a model of their effect on export efficiency (*ef*, the ratio of the flux of organic matter exported across the base of the euphotic zone to the integrated primary production within that layer) explains the observed dependence of *ef* on temperature (Cael and Follows 2016).

Here we ask: how has the documented trend in global ocean temperatures over the past few decades impacted the efficiency of this export flux? We use temperature records with the above model to infer temperature's contribution to global change in *ef* through time. We focus on multidecadal changes (after Henson et al. 2010) over the past 33 yr (the duration over which suitable data products are available) using multiple data products to examine the sensitivity of calculated changes to inputs used.

A metabolic model of export efficiency

Export efficiency is a combination of growth, respiration, sinking, remineralization, and other processes. It has primarily been considered as a function of temperature (T), primary production ($\mathcal{P}$), and community structure (i.e., the size distribution of plankton, who is eating whom, and so forth) (Michaels and Silver 1988; Eppley 1989; Laws et al. 2000). While all three are important, community structure variables and their influence on *ef* are challenging to assess, quantify, and measure, making an estimation of how recent climatic shifts have produced global shifts in *ef* via community structure challenging. Previous studies disagree substantially on both global trends in $\mathcal{P}$ (Siegel et al. 2013; Behrenfeld et al. 2016; and references therein) and the relationship between *ef* and $\mathcal{P}$ (Buesseler 1998; Laws et al. 2011; Maiti et al. 2013), making an estimation of how climatic shifts have affected *ef* via $\mathcal{P}$ similarly intractable.

In contrast, global trends in sea surface temperature (SST) over the past few decades are well-characterized (IPCC 2014). SST is commonly used as a proxy for upper-ocean temperature, is anticorrelated with *ef* (e.g., Laws et al. 2000; Henson et al. 2011), and is also one of the only variables for which long-term, global observational records exist (Ishii et al. 2005; Reynolds et al. 2007; Dee et al. 2011). Do SST observations, suggest a shift in *ef*?

Recently, a simple model was proposed (Cael and Follows 2016; herein the model will be referred to as CF16) to explain the *ef*-*T* relationship seen in observations. Heterotrophic and phototrophic growth rates increase with temperature, but the former increase more so (Eppley 1972; Huntley and Lopez 1992); metabolic ecological theory relates this to the different activation energies of respiration and photosynthesis (Lopez-Urrutia et al. 2006). As originally posited in Laws et al. (2000), this differential dependence suggests that increasing temperatures should increase community respiration relative to production and therefore decrease *ef*. Rather than absorbing these dependencies into a numerical food-web model as in Laws et al. (2000), CF16 considers *ef* as a random variable scaled by temperature according to these dependencies, and this description is shown to be consistent with observations. We refer the reader to Cael and Follows (2016) for a full description and discussion of CF16, but describe it briefly below.

Within a basic differential equation for plankton biomass p in the euphotic layer,

$$\dot{p} = \mu p - \lambda p - \lambda' p - wp \tag{1}$$

where μ is the growth rate, λ is the grazing rate, λ' is the loss rate due to factors other than grazing, and w is the sinking rate, in steady state $ef = \frac{wp}{\mu p}$ can be written as

$$ef = 1 - \frac{\lambda + \lambda'}{\mu} \tag{2}$$

Then one can find the maximum efficiency by neglecting λ' and incorporating the temperature dependencies of phototrophy and heterotrophy as $\mu \propto e^{0.063T}$, $\lambda \propto e^{0.11T}$. This yields a curve of maximum export efficiency as a function of temperature:

$$ef_{\max}(T) = 1 - \alpha e^{\beta T} \tag{3}$$

where the parameter* α is one minus the maximum efficiency at $T = 0$, which is estimated empirically to be $\alpha = 0.24$, and the parameter $\beta = 0.11 - 0.063 = 0.047$. *ef* values can be rescaled by $ef_{\max}(T)$ to extract this temperature dependence; that is, $ef / ef_{\max}(T)$ is variable but independent of temperature, suggesting that this rescaling captures all of the temperature dependency of *ef* (Cael and Follows 2016).

Here we then use this temperature scaling to derive an average $\langle ef \rangle$ as a function of temperature†:

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*Figure S1 (*see* Supporting Information) shows the sensitivity of CF16 to changes in the parameters α and β.

$^{\dagger}\langle \widetilde{ef} \rangle = 0.37$ for the observations used in Cael and Follows (2016) so we use that value here nominally, though we note the value of this factor is largely irrelevant for the analyses of this paper because we focus on percent changes.

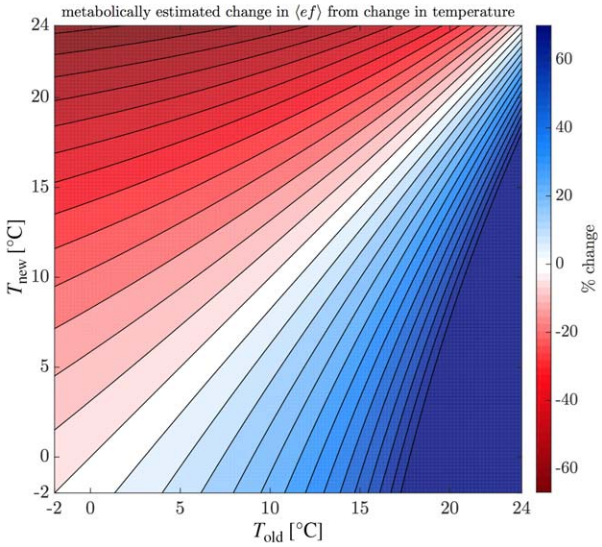

Fig. 1. Percent change in $\langle ef \rangle$ after a temperature change, as estimated by CF16 (see Eq. 3), as a function of the initial and final temperatures (T_{old} and T_{new}). Contours are spaced at 5%.

Table 1. Percent change in $\langle\langle ef \rangle\rangle$, during the period 1982–2014, as estimated by CF16, for different data products. All changes suggest a decrease in $\langle\langle ef \rangle\rangle$ and are statistically significant ($p < 0.001$; *see* Supporting Information). Mean and standard deviation of percent change across each SST-$\mathcal{P}$ pair are $-1.5\% \pm 0.4\%$.

SST	$\mathcal{P}$	% Change
ERA	CbPMv2	−0.83
ERA	VGPM	−1.12
COBE	CbPMv2	−1.55
COBE	VGPM	−1.98
OISST	CbPMv2	−1.52
OISST	VGPM	−1.91

$$\langle ef \rangle(T) = \langle \tilde{ef} \rangle \times ef_{\max}(T). \tag{4}$$

While empirical models have been proposed to relate temperature to *ef* (Laws et al. 2000, 2011; Dunne et al. 2005; Henson et al. 2011), we focus on CF16 because it isolates a single, understood metabolic mechanism—the hypothesized and observed differential response of temperature on phototrophic and heterotrophic metabolisms. We emphasize that CF16 does not seek to be a complete model for or explain all the variability in *ef*; it isolates the variability in *ef* due to the differential temperature effect on metabolism. Because the differential temperature response is assumed to arise from chemical kinetics, namely the activation energies of respiration and photosynthesis, it is assumed to be constant over time.

Figure 1 shows the estimated percent change of $\langle ef \rangle$ resulting from a temperature change from T_{old} to T_{new} as predicted by CF16. Percent changes are a function of both, and as Eq. 4 varies by a factor of three from low to high temperatures, percent changes in response to large temperature differences can be very large. Note that temperature differences shown in Fig. 1 are larger than those that have been observed over the past 33 yr, which are <1°C (IPCC 2014).

Global estimates of multidecadal change in ef

CF16 can be used to calculate $\langle ef \rangle$ from SST,[‡] so it can be used to infer trends in globally averaged *ef* (for which we will use the symbol[§] $\langle\langle ef \rangle\rangle$) from SST reanalyses. Does CF16 indicate a trend? Is this trend consistent between data products?

To test these questions, we generate three time series of $\langle ef \rangle$ from different SST reanalyses and Eq. 4. We use the ECMWF ERA-Interim SST (Dee et al. 2011), the NOAA OISST (Reynolds et al. 2007), and the ESRL COBE-SST (Ishii et al. 2005) products. Description and discussion of how these reanalyses are developed can be found in the above references. For consistent comparison, we use a common

- spatial resolution of 1°, the resolution of the coarsest product
- temporal resolution of 1 month, i.e., monthly averages available for each product
- start time of January 1982, the January of the earliest year common to all three products
- end time of December 2014, the December of the latest year common to all three products

From each SST product we compute global time series of $\langle ef \rangle$ for each 1° bin.

Because we define $\langle\langle ef \rangle\rangle$ as the ratio of globally integrated export flux to globally integrated production, to compute it $\langle ef \rangle$ for each 1° bin must be weighted by both area and $\mathcal{P}$. We use climatologies[¶] from the two most common algorithms to estimate $\mathcal{P}$: the Carbon-based Productivity Model (CbPMv2) (Westberry et al. 2008), and the Vertically

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[‡] As a proxy for upper-ocean temperature.

[§] All export efficiency notation: $ef :=$ export flux divided by primary production. $\mathcal{P} :=$ primary production. $T :=$ temperature. $ef_{\max}(T) :=$ theoretical maximum *ef* for a given temperature. $\alpha = 0.24$: one minus the maximum efficiency at $T = 0$, $\beta = 0.047$: the differential temperature sensitivity of phototrophy and heterotrophy. $\tilde{ef} := ef / ef_{\max}(T)$. $\langle ef \rangle :=$ mean *ef* averaged over a spatial region, e.g., a 1° box or a latitudinal band. $\langle\langle ef \rangle\rangle :=$ globally averaged *ef*.

[¶] Both available at http://www.science.oregonstate.edu/ocean.productivity/standard.product.php. We use climatologies rather than time series because of the lack of $\mathcal{P}$ time series over the duration of the SST time series. This is justifiable in light of the disagreement on global trends in $\mathcal{P}$ (Siegel et al. 2013; Behrenfeld et al. 2016).

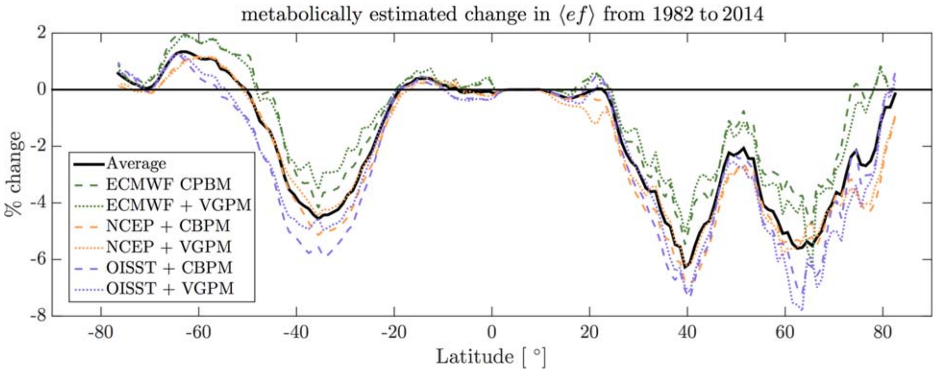

Fig. 2. Percent change in ⟨*ef*⟩ from 1982 to 2014, as estimated by CF16, as a function of latitude, for different data products. Color corresponds to SST product and line type to $\mathcal{P}$ product. Black curve is the average across the SST-$\mathcal{P}$ pairs.

Generalized Productivity Model (VGPM) (Behrenfeld and Falkowski 1997). In total, the time series $\langle\langle ef\rangle\rangle(t)$ is calculated by

$$\langle\langle ef\rangle\rangle(t) := \frac{\sum_{x,y} A(x,y)\mathcal{P}(x,y,t \bmod 12)\langle ef\rangle(x,y,t)}{\sum_{x,y} A(x,y)\mathcal{P}(x,y,t \bmod 12)} \quad (5)$$

where (x, y) are latitude and longitude, $A(x, y)$ is the area of the 1°×1° box at (x, y), and t mod 12 is the month of the $\mathcal{P}$-climatology.

The above three SST and two $\mathcal{P}$ products yield six time series of $\langle\langle ef\rangle\rangle(t)$. We regress each against time using the simplest statistical model that resolves a seasonal cycle and a linear trend:

$$\langle\langle ef\rangle\rangle(t) = mt + b(\text{month}) + \text{error} \quad (6)$$

regressing $\langle\langle ef\rangle\rangle(t)$ against a time variable that runs $t=1, 2, \ldots$ along with an indicator variable for each month (*see* Supporting Information). To estimate statistical significance of the trends, we use both the standard method and two resampling methods, one of which accounts for autocorrelation in the time series (*see* Supporting Information). The estimated rates of change m can be multiplied by the duration of the time series to estimate a percent change in $\langle\langle ef\rangle\rangle(t)$ from 1982 to 2014 for each SST-$\mathcal{P}$ pair; *see* Table 1.

Independent of SST and $\mathcal{P}$ product, a global decline in $\langle\langle ef\rangle\rangle$ is observed of 1.5% ± 0.4%, where the uncertainty is the standard deviation across SST-$\mathcal{P}$ pairs. All declines are found to be significant ($p < 0.001$) by all three significance estimation procedures. Over the entire timeseries, CF16 predicts a $\langle\langle ef\rangle\rangle$ value of 0.128 ± 0.016.

How consequential is a 1.5% ± 0.4% decrease in $\langle\langle ef\rangle\rangle$? A simple box model of the carbon cycle (Ito and Follows 2005; Williams and Follows 2011; *see* Supporting Information) suggests a 1.5% ± 0.4% decline in $\langle\langle ef\rangle\rangle$ would result in a 1.2% ± 0.3% increase in the mixing ratio of atmospheric CO_2 on millennial timescales (when the solubility pump has equilibrated but prior to carbonate compensation). Generalizing this result, the sensitivity of the soft-tissue carbon pump to changes in mean sea surface temperature is predicted to be $\sim$ 7 ppm K^{-1}, comparable to the $\sim$ 10 ppm K^{-1} sensitivity of the solubility pump to global mean ocean temperature suggested by theory and models (Williams and Follows 2011, their Fig. 13.9b). Interestingly, the combined sensitivity of solubility and metabolic effects predicts a $\sim$ 70 ppm drawdown of atmospheric CO_2 for a 4K global cooling of the ocean associated with the last Glacial Maximum (Adkins et al. 2002).

We note that substantial latitudinal variation in SST trends have occurred during the record of these SST reanalyses. Thus, we employ the same procedure as above, but only averaging zonally, yielding an estimated percent change in ⟨*ef*⟩ (here the ratio of longitudinally integrated export flux to longitudinally integrated production) at each degree of latitude from 1982 to 2014. See Fig. 2; substantial latitudinal variation exists, with percent changes ranging between +2% and −8%. ⟨*ef*⟩ in the Southern Ocean increases slightly, corresponding to cooling, while ⟨*ef*⟩ changes little in the tropics where SST is high. Thus, it appears the global decrease of 1–2% is driven by decreases in the Arctic and at midlatitudes, where ⟨*ef*⟩ decreases on the order of 5%. While variation exists between each of the six SST-$\mathcal{P}$ pairs, their latitudinal dependence is similar.

Conclusion

Neither the existence, magnitude, nor driving mechanisms of a change in the biological pump over the past few decades of recent climate change can be established definitively. This is an unavoidable result of searching for small shifts in a system exhibiting substantial variability on all time scales that is challenging to measure adequately.

A simple metabolic perspective accounting for the differential temperature dependencies of autotrophy and heterotrophy underpins a model of export efficiency, which explains its observed dependence on temperature. Driving that model with observed changes in SST leads to a suggestion that global export efficiency has decreased 1.5% ± 0.4% over the past few decades, with larger decreases in midlatitudes and Arctic. This decrease is robust across SST and primary production data products. Larger temperature differences than those observed over the past few decades are predicted to cause larger changes in global export efficiency.

References

Adkins, J. F., K. McIntyre, and D. P. Schrag. 2002. The salinity, temperature and $\delta^{18}O$ of the Glacial deep ocean. Science **298**: 1769–1773. doi:10.1126/science.1076252

Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. **42**: 1–20. doi:10.4319/lo.1997.42.1.0001

Behrenfeld, M. J., and others. 2016. Revaluating ocean warming impacts on global phytoplankton. Nat. Clim. Chang. **6**: 323–330. doi:10.1038/nclimate2838

Boyd, P. W. 2015. Toward quantifying the response of the oceans' biological pump to climate change. Front. Mar. Sci. **2**: 77. doi:10.3389/fmars.2015.00077

Boyd, P. W., and T. W. Trull. 2007. Understanding the export of biogenic particles in oceanic waters: Is there consensus? Prog. Oceanogr. **72**: 276–312. doi:10.1016/j.pocean.2006.10.007

Buesseler, K. O. 1998. The decoupling of production and particular export in the surface ocean. Global Biogeochem. Cycles **12**: 297–310. doi:10.1029/97GB03366

Buesseler, K. O., and P. W. Boyd. 2009. Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean. Limnol. Oceanogr. **54**: 1210–1232. doi:10.4319/lo.2009.54.4.1210

Cael, B. B., and M. J. Follows. 2016. On the temperature dependence of oceanic export efficiency. Geophys. Res. Lett. **43**: 5170–5175. doi:10.1002/2016GL068877

Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature **408**: 184–187. doi:10.1038/35041539

Dee, D. P., and others. 2011. The ERA-Interim reanalysis: Configuration and performance of the data assimilation system. Q. J. R. Meteorol. Soc. **137**: 553–597. doi:10.1002/qj.828

Dunne, J. P., R. A. Armstrong, A. Gnanadesikan, and J. L. Sarmiento. 2005. Empirical and mechanistic models for the particle export ratio. Global Biogeochem. Cycles **19**: GB4026. doi:10.1029/2004GB002390

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. **70**: 1063–1085.

Eppley, R. W. 1989. New production: History, methods, problem, p. 85–97. *In* W. H. Berger, V. S. Smetacek, and G. Wefer [eds.], Productivity of the ocean. John Wiley.

Henson, S. A., J. L. Sarmiento, J. P. Dunne, L. Bopp, I. Lima, S. C. Doney, J. John, and C. Beaulieu. 2010. Detection of anthropogenic climate change in satellite records of ocean chlorophyll and productivity. Biogeosciences **7**: 621–640. doi:10.5194/bg-7-621-2010

Henson, S. A., R. Sanders, E. Madsen, P. J. Morris, F. Le Moigne, and G. D. Quartly. 2011. A reduced estimate of the strength of the ocean's biological carbon pump. Geophys. Res. Lett. **38**: L04606. doi:10.1029/2011GL046735

Huntley, M. E., and M. D. Lopez. 1992. Temperature-dependent production of marine copepods: A global synthesis. Am. Nat. **140**: 201–242. doi:10.1086/285410

IPCC. 2014. Climate Change 2014: Synthesis Report. *In* Core Writing Team, R. K. Pachauri, and L. A. Meyer [eds.], Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, 151 pp. IPCC, Geneva, Switzerland.

Ishii, M., A. Shouji, S. Sugimoto, and T. Matsumoto. 2005. Objective analyses of sea-surface temperature and marine meteorological variables for the 20th century using ICOADS and the Kobe collection. Int. J. Climatol. **25**: 865–879. doi:10.1002/joc.1169

Ito, T., and M. J. Follows. 2005. Preformed phosphate, soft tissue pump and atmospheric CO_2. J. Mar. Res. **63**: 813–839. doi:10.1357/0022240054663231

Laws, E. A., P. G. Falkowski, W. O. Smith, H. Ducklow, and J. J. McCarthy. 2000. Temperature effects on export production in the open ocean. Global Biogeochem. Cycles **14**: 1231–1246. doi:10.1029/1999GB001229

Laws, E. A., E. D'Sa, and P. Naik. 2011. Simple equations to estimate ratios of new or export production to total production from satellite-derived estimates of sea surface temperature and primary production. Limnol. Oceanogr.: Methods **9**: 593–601. doi:10.4319/lom.2011.9.593

López-Urrutia Á., E. San Martin, R. P. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. Proc. Nat. Acad. Sci. **103**: 8739–8744.

Maiti, K., M. A. Charette, K. O. Buesseler, and M. Kahru. 2013. An inverse relationship between production and export efficiency in the Southern Ocean. Geophys. Res. Lett. **40**: 1557–1561. doi:10.1002/grl.50219

Michaels, A. F., and M. W. Silver. 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Res. Part A **35**: 473–490. doi:10.1016/0198-0149(88)90126-4

Reynolds, R. W., T. M. Smith, C. Liu, D. B. Chelton, K. S. Casey, and M. G. Schlax. 2007. Daily high-resolution-blended analyses for sea surface temperature. J. Clim. **20**: 5473–5496. doi:10.1175/2007JCLI1824.1

Siegel, D. A., and others. 2013. Regional to global assessments of phytoplankton dynamics from the SeaWiFS mission. Remote Sens. Environ. **135**: 77–91. doi:10.1016/j.rse.2013.03.025

Volk, T., and M. I. Hoffert. 1985. Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO_2 changes, p. 99–110. *In* E. T. Sundquist and W. S. Broecker [eds.], The carbon cycle and atmospheric CO_2: Natural variations archean to present. Washington, DC: American Geophysical Union.

Westberry, T., M. J. Behrenfeld, D. A. Siegel, and E. Boss. 2008. Carbon-based primary productivity modeling with vertically resolved photoacclimation. Global Biogeochem. Cycles **22**: GB2024. doi:10.1029/2007GB003078

Williams, R. G., and M. J. Follows. 2011. Ocean dynamics and the carbon cycle. Cambridge Univ. Press.

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